THE NUMERICAL INTENSITY OF FAUNAS.[1]

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In the various aspects of the Development of Life upon the earth the attention of the student has been principally directed to the question of form, as a problem of derivation. The external configuration of the enclosing frame-work or envelopes of organisms, or the modified outlines of internal skeletons have been closely compared, and species have been defined upon their differences, and the record of the march of specific change, group segregation and class development compiled from their study. The enumeration of species as they multiply, or decrease and disappear has been made, and the successive expansions and contractions of the lineal avenues of descent extensively elaborated. The student has less frequently been brought to consider the question of number, the numerical increase of forms, or to attach any biological significance to the arithmetical rise or decrease of species. It is, upon a little reflection evident that the subject of numbers, if it admits of any determination, may have or must have, a direct connexion with the ease and spontaneity with which a new or old species maintains itself, and may prove an index of the severity of competition or of the difficulty of living in its field of zoological activity.

Assuming the rate of increase uniform, the apparatus and impulse to procreation identical in a number of species, that one, of course, will survive in the greatest numbers whose life is attended with the least friction, against whose functions and habits the smaller array of obstacles active and passive exist. The comparison of species in this respect, so far as it is used to make out the comparative adaptation of species to certain conditions, assumes of necessity an identical fecundity in each species, and the comparison has, therefore, valid probability between species of the same families, or genera or perhaps classes.

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On the other hand a more recondite suggestion is made in this inquiry. Favorable conditions for the multiplication of a species, such as temperature, food-supply, freedom from enemies, habitability of station, etc., naturally assist numerical increase. But the speculation suggests differences in the time required for a species to attain *momentum*, the time required for it to reach the maximum rate of increase, when its vitality has attained such force as to most effectually overcome hampering conditions, and is recorded in the number of individuals produced at one period. This question touches the surmises made as to the manner of specific introductions. Does a species make its appearance in one example—as an individual—on the world's stage or, if dicœcious, in pairs, and then proceed to establish its currency, and so in geometrical ratio of increase engage itself in subjugating its environment and dispersing or suppressing its competitors? Or do species appear in numbers, and from separated points of occupation begin spreading, until their divided areas coalesce, and their geographical coincides with their numerical maximum? Or finally does the manner of their entrance into life vary for different species, or the species of different groups in both these ways? It seems probable that the higher orders of animals—especially the vertebrates—are *sporadic* in their appearance, viz., differentiate as individuals, while the lower are *massive*, viz., differentiate in hosts.

Conditions being equal the invertebrates should reach their numerical maxima quicker than the higher vertebrates, and their maxima should, comparatively, reach enormously higher figures. What the functional activity of procreation in a new species is, cannot be determined. It would seem probable that if specific variation were a process of insensible or slightly sensible changes in forms or external physical features, the correlated disturbances of function would be imperceptible and the new species would carry on the work of self-propagation with the same energy as the allied species amongst whom it makes its appearance. The actual numerical results would be at first low, because of the smaller number of individuals of the new species and would increase as that number enlarged,

and the opportunities or occasions of procreation multiplied. Again it is necessary to consider a reversal of this. The sterility of the offspring of crossed parents of different species points to the fact that there are or may be functional changes in the powers of generation, and that the new species, is, by this law, made dependent for its successful extension, upon the intercourse of similar individuals. It is likely that in connection with the rise of a new species those organs concerned in reproduction have become modified, and the system of seminal secretion, which carries with it the power of perpetuating the new forms, has itself been more or less profoundly affected. From such considerations it seems fairly probable that new species appear in limited numbers, and acquire after time the full power of propagation until with increasing numbers the maximum of their numerical rise is reached, and then that decadence begins which ends in their disappearance. It will be understood that by "limited numbers" we mean such representations of species as are much below their later and more normal development.

It then appears from such considerations, without further detail, that the factors of numerical increase are two, the external or physical conditions of life, and the internal or biogenetic force of propagation. As regards the first, the external or physical conditions of life, it may be assumed that the appearance of a species must take place under favorable conditions, if we are to accept the Darwinian hypothesis, that specific origination means that very thing, the better adaptation of new species to reigning conditions than any other, for it is its preponderant aptitude for life under these conditions that brings the new species into existence. So that as regards the encouragement to increase given by the external conditions it is unexceptional or adequate, and the rate of multiplication is then made dependent upon the physiological factor, the power and provision for propagation. These favorable conditions will be temporary. They will be succeeded by others less favorable, and the species, started under way under the best external auspices will begin to work against physical detriments and brakes that will lower its vital momentum, and, unless

the biogenetic factor keeps up or even becomes intensified, the species begins its downward course, since numerical diminution means final extinction. The biogenetic factor, the influence of propagation, will, in all probability, decline with any changes in external conditions which affect the physical well-being of the organism, so that the sum of influences springing from external circumstances and internal conditions work conjointly to exhilerate or depress the life of the animal. Furthermore, although a new species responds more fittingly to its environment and possesses peculiar advantages over its companions, this species, it may be assumed, survives because it is less at odds with its surroundings, not because it is most appropriately placed. As it becomes more and more part of the new status which brought it into existence, its organism more and more nearly attains its limital fecundity.

The list of possible combinations of conditions upon the emergence of a species would then be four.

First.—Favorable Environment and High Vitality=procreative activity.

Second.—Unfavorable Environment and High Vitality.

Third.—Favorable Environment and Low Vitality.

Fourth.—Unfavorable Environment and Low Vitality.

The discussion of these four *as limital expressions*, covers the varying phases under which a species attains its numerical maximum. And this discussion assumes, for the sake of reaching definite results, that the species is considered as restrained by the boundaries of a limited area, an assumption not very much at variance with facts.

Favorable Environment and High Vitality.—In this case the species would rapidly rise to its numerical maximum, and maintain it as long as the environment and its own vitality remained propitious. But this very intensity of development would lead to the deterioration of the species, and bring about its own extinction. The competition between its own representatives would become exasperated through their great number, and this would drain the food-supply, while the excessive productivity would reduce procreative power. The zoological consequence, in this instance, would be quick

numerical expansion followed by a more or less abrupt decline. Darwin says (Origin of Species Chap. X, 1860). "There is reason to believe that the complete extinction of the species of a group is generally a slower process than their production; if the appearance and disappearance of a group of species be represented as before by a vertical line of varying thickness, the line is found to taper more gradually at its upper end, which marks the progress of extermination, than at its lower end, which marks the first appearance and increase in numbers of the species." In the case of favorable environment and high vitality the line would probably begin suddenly with a thickened end, continued and increased for some distance, and slope steeply to its termination. Two examples in paleontological history illustrate this; the Trilobitic fauna of the Upper Cambrian, the Potsdam of Wisconsin and Minnesota, and the successive Ammonitic faunas of the Jura-Lias in Europe.

Prof. Hall recognized and tentatively separated three horizons of the trilobitic beds of Wisconsin and Minnesota; the earlier trilobites were referable in numbers to the genus *Conocephalites* while *Dicelocephalus* emerges in the middle beds and becomes numerically important through these and the higher beds. Prof. Hall was struck with their extreme abundance, and records his own impressions in these words; "the multitude of individuals of a few species is really wonderful; for in some beds the layers may be separated at every inch, or even half inch, and yet the entire surface is covered with the dismembered parts of these ancient trilobites." As to the Ammonites of the Jurassic they are celebrated for the sharpness of lines of demarkation between beds abounding in great numbers of the different species.

Unfavorable Environment and High Vitality.—In this case there would result a variable numerical abundance according to the equilibrium established between these discordant factors, but the average result would be a numerical uniformity extended over a considerable length of time. The procreative power would replenish the losses by death, and keep up, at least at first, a uniform amplitude of life. The unfavorable environment would work a defeating influence upon procrea-

tion, and after a length of time, bring about a low vitality which in conjunction with the uncongenial surroundings would wind up the species.

Of course the term *unfavorable* is here used comparatively, not meaning *inimical*, because a new species upon the doctrine of adaptation could not arise in hostile circumstances, but meaning less favorable than the *most* auspicious surroundings. The result as measured in numerical estimates would be a low mean, which perhaps as the environment improved might increase. It is only likely that such conditions are present when a species migrates, or is invaded by a change of physical conditions less advantageous than those it has previously enjoyed. A new species with high vitality is hardly consistent with unfavorable environment at the beginning, and the category we are considering would only be exemplified in the numerical exhibit of species whose habitat has been affected unfavorably. The repression of great numbers of individuals at any one time would tend to lengthen the life of the species, inasmuch as it would relieve it from struggle in its own midst, and this would have a tendency to extend its days.

In the paleontological record the case of *Atrypa reticularis* seems to illustrate this numerical constancy. From the Upper Silurian in the Niagara through the Lower Helderberg, Oriskany Schoharie and Upper Helderberg it keeps up a more or less uniform though not excessive representation until diverging in the Devonian into *A. vexata* and *A. spinosa* it becomes itself more numerous seeming then to pass under the conditions of the first category—high vitality and favorable environment—and declining rapidly terminates in the Upper Hamilton. *Atrypa reticularis*, as is well known, does not attain a large size in the Silurian, but, according to Hall, exhibits considerable variety of form. It is in the stage of "*oscillation*," not yet having attained specific fixity and this fact of formal instability points to a lack of congruity between itself and its environment and leads us to consider it an example under this heading.

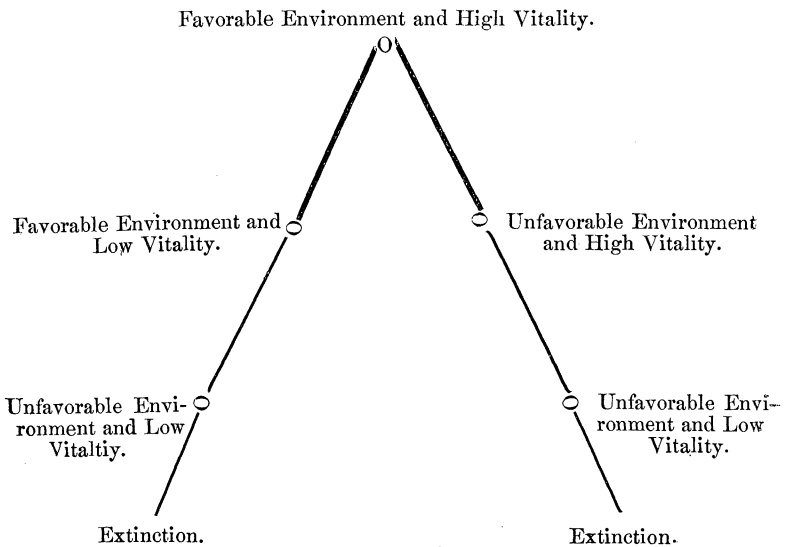
Favorable Environment and Low Vitality.—By "Low Vitality" we here designate a certain sluggishness in fecundity in cer-

tain animals though the value of the procreative energy considered at the instant of its exercise may be high. Evidently for such animals their duration in time will be conditioned largely upon favorable circumstances of life and without these they must undergo extinction. The numerical representation must always be small; it is essentially limited by their intrinsic predisposition to be slow breeders. This assumption seems applicable to species which without any apparent change in their environment become subject to a progressive failure in numbers. The history of invertebrate life on the earth's surface emphasizes this. Throughout similar conditions or what, from lithological evidence, seem *identical* conditions, species dwindle and disappear. On what hypothesis can this gradual vanishment be explained, except that the living momentum has run down, a physiological deterioration has set in, which must, no matter how auspicious be the physical requirements, compass the discomfiture and suppression of the species. Low vitality might also reasonably imply a certain functional weakness which affects the organic intregrity of a species. Under either implication, that of low procreative power or functional weakness, favorable environment fictitiously prolongs the life of the species and gives a deceptive appearance of stability to a species internally disintegrating. Its numerical ratio must be a reduced one.

Unfavorable Environment and Low Vitality.—This category symbolizes the rapid decline of a species, and is symptomatic of the final stages in its life-history. Where unfavorable conditions combine with intrinsic decrepitude the doom of a species is quickly sealed, and it vanishes from the scene scarcely noticed amidst the on-coming armies of new and intense competitors.

These four categories which we have epitomized, embodying the relations of *vitality* to *environment* and applied to the phenomena of the numerical abundance of a species, may be generally regarded as the formal stages of a species' decline. And we observe that the succession of these stages may follow one of two directions as divergent lines from an original condition. That original condition is *Favorable Environment and*

High Vitality, for while these terms may not be co-existent upon the first appearance of a species they must quickly become so. A species originates, if we are to accept the Darwinian hypothesis by reason of its preponderant adaptation to new conditions, and if at first that adaptation is tentative or accidental, it soon becomes assured and necessary, upon the *settling down* of species and environment into a complete reciprocity. We then may expect two similar but contrasted stages to succeed this original, initial state, as is seen in the subjoined diagram; these stages presenting equivalent *numerical* zones, to be followed by two similar and identical stages, which in turn precede the extinction of the species.



The conjecture here delineated shows a species beginning under the favoring conjunction of vitality and adapted environment, rising in *numerical intensity* until a weakening of these elements sets in, and the species begins to decline in numbers. It may decline along a line of lessening vitality with environment constant, or, it may decline along a line of increasingly hostile surroundings with vitality constant, and it may be assumed that a stage of equipoise may be reached along either

of these lines wherein, however, the factors of environment and vitality are oppositely related. There would then be two stages of equal numerical efficiency, opposite in conditions but equivalent in effects, favorable environment and low vitality, and unfavorable environment and high vitality, and succeeding these as an inevitable sequence comes at the end of either road of retreat, the final stage of unfavorable environment and low vitality and the extinction of the species. Along either of the avenues of deterioration the numerical intensity is supposed to decline similarly but this superficial resemblance covers a radical contrast of agencies and we are brought to consider two kinds of strain; the strain of internal weakness, and the strain of external disparity. This introduces a crucial question we think in reference to the Darwinian hypothesis. That hypothesis assumes that species are perpetuated by the concordance declared between them and their surroundings, and it seems enclosed in this wide opening statement, that the Darwinian must allow a certain power of *provocation* upon organisms from exterior conditions, viz., that the inherent variability (fully emphasized by Darwin) of organisms is stimulated by changing environment while it should be more quiescent under unchanged circumstances of life. Without at present pressing this question the inference, we think, is reasonable. Therefore, in establishing a line of numerical decline for a species we have in this suggestion a form of test as to whether that decline arises from changing environment or changing vitality. If it proceeds from changing environment it will be, upon the Darwinian theory, accompanied by specific offshoots, and the disappearing species will sink from sight amidst the emergence of related species; but, if it proceeds from devitalization it will display a species dying as it were alone, unattended by the growth of related varieties, and passing away without those bequests of derivative forms which, in the other instance, represent the yet internally vigorous species struggling to maintain its empire under the guise of modified offspring. These propositions will, it may perhaps be conceded, repay more careful and detailed application to zoological history, as it has been written in the successive ages of geology.